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Territorial defence in a network: audiences only matter to male fiddler crabs primed for confrontation

Lay Summary: Being part of a social network means that responses to social confrontations are likely to be more complex than they might seem. Indeed, here we find effects of a wider network of conspecifics on an individual's behaviour in male European fiddler crabs. Males became more aggressive toward intruders if their neighbour was watching when they had previously observed an aggressive interaction between their neighbour and a male territory intruder.

Abstract

Territorial contests often occur in the presence of conspecifics not directly involved in the interaction. Actors may alter their behaviour in the presence of this audience, an 'audience effect', and audiences themselves may alter their behaviour as a result of observing an interaction, a 'bystander effect'. Previous work has documented these effects by looking at each in isolation, but to our knowledge, none has investigated their interaction; something that is more likely to represent a realistic scenario for species where individuals aggregate spatially. We therefore have a somewhat limited understanding of the extent and direction of these potentially complex indirect social effects on behaviour. Here we examined how audience and bystander effects work in tandem to modify resident male aggressive behaviour towards intruders in European fiddler crabs, *Afruca tangeri*. We found that male crabs with an audience showed greater aggressive behaviour towards an intruder compared to males without an audience, but only if they had acted as a bystander to an aggressive signalling interaction prior to the intrusion. Indeed, bystanding during aggressive interactions elevated

aggressive responses to intruders maximally if there was an audience present. Our results suggest that bystanding had a priming effect on territory-holding males, potentially by providing information on the immediate level of competition in the local neighbourhood, and that same-sex audiences only matter if males have been primed. This study highlights the fundamental importance of considering broader interaction networks in studying real-world dyadic interactions and of including non-vertebrate taxonomic groups in these studies.

Key words: audience effect, bystander effect, invertebrate, fiddler crab, *Afruca tangeri*, *Uca tangeri*

Background

Considering communication in the context of a wider network has revealed behaviours and effects such as eavesdropping, audience effects and bystander effects, that would not be observable from a dyadic approach (McGregor, 2005). Territorial contests are typically settled through pair-wise interactions within a network of multiple individuals, rather than in (McGregor and Dabelsteen, 1996). Audience effects occur when animals modify their behaviour due to the presence of other individuals not involved in the interaction (Zuberbühler, 2008) and these effects have been shown to alter the intensity of agonistic displays in a number of species (Cruz and Oliveira, 2015; dos Santos et al., 2017; Fitzsimmons and Bertram, 2013; Montroy et al., 2016; Setoguchi et al., 2015). In the context of territorial defence, the audience effect has been demonstrated to be dependent not only on the sex of the audience, but also on the territorial status and familiarity of individuals in the wider network (Bertucci et al., 2014; Dzieweczynski et al., 2005). Observed differences in behaviour in the presence of an audience suggest that individuals can (1) assess attributes of their audience and (2) adjust their behaviour as a strategy to counter costs (or strengthen benefits) that can come with eavesdropping, or more generally, gathering of social information by audiences (Earley and Dugatkin, 2002). In the bystander effect the audience members themselves are influenced by observing an interaction (Earley and Dugatkin, 2002; Oliveira et al., 2001; Peake et al., 2006). The observation acts directly on the motivational system (Hirschenhauser and Oliveira, 2006; Oliveira et al., 2001) and prepares individuals for what may happen next in their social environment (Antunes and Oliveira, 2009). Individuals can, for example, be primed to augment their levels of aggression in interactions following bystanding. For example, Clotfelter and Paolino (Clotfelter and Paolino, 2003) found increased aggressiveness by Siamese fighting fish, *Betta splendens*, towards a novel male

conspecific after the observation of an aggressive interaction. However, reverse priming, a reduction in aggressive behaviour, has also been found, for example, in a study of crayfish, *Orconectes rusticus* (Zulandt et al., 2008), which to our knowledge is also the only invertebrate species in which bystander effects have been investigated.

Although audience and bystander effects are frequently documented, it is not clear from the literature how bystander and audience effects may interact. This represents a potential key gap in our understanding of the strength or importance of these effects in *in situ* contexts where they are likely to happen concurrently, particularly in species where individuals live in aggregated communities. A study in Siamese fighting fish, suggests that simply viewing an unfamiliar male prior to a contest with another male can prime males for increased aggression during a fight, irrespective of whether the audience is present or not during the fight itself (Matos et al., 2003). It also highlights the complexity of bystander and audience effects and the need to manipulate these effects in tandem in order to deepen our understanding of the significance of dynamics in the social environment for the expression of behaviour. Here we investigate the interplay between audience and bystander effects on the territorial behaviour of male European fiddler crabs, *Afruca tangeri*. Fiddler crabs are very unlikely to be found in isolation (Pope, 2005), and therefore have a high likelihood of engaging in social interactions with multiple receivers within signal range. Males actively defend territories around their burrows (Hemmi and Zeil, 2003) with their one greatly enlarged claw, used for the production of highly conspicuous visual agonistic and courtship signals and for fighting (Oliveira and Custódio, 1998; Wolfrath, 1993). Male crabs without a burrow will wander through the population and challenge burrow holders in attempts to acquire a burrow (Jordao and Oliveira, 2005). Burrow holding males must therefore invest in an agonistic response in order to retain residency (Oliveira and Custódio, 1998). Recent work in another fiddler crab

species suggests that same-sex audiences do not matter for expressed levels of aggression (dos Santos et al., 2017), given the ubiquity of males in the immediate social environment (i.e. males are highly likely to have male neighbours), this is perhaps not surprising. We propose instead that males will fine-tune their responsiveness to their social environment according to current social information, such as the immediate level of competition in the neighbourhood. If males observe a territorial dispute in their neighbour's territory, they should be primed for a possible challenge of their own territory and therefore will be more responsive or sensitive to their immediate social environment. In this case, bystanding to an aggressive interaction between a neighbouring male and a stranger (intruding male), should augment the aggressive response exhibited by males towards intruders appearing close in time. This should be particularly so when the social stimuli are increased by a male audience as this audience can gather information on the interaction outcome (e.g., the competitive ability of his male neighbour) and in the least, acts as an indicator of a more competitive social environment (i.e. more males are present) than when no male audience is present. In this investigation, we used an *in situ* experimental manipulation of the social environment that burrow holding male crabs experienced to test such effects during territorial confrontations in the home environment.

Methods

The study was carried out in the Parque Natural da Ria Formosa, Portugal (N370927, E073244) from May to July 2012 in order to quantify audience and bystander effects *in situ* in males of a free roaming population of European fiddler crabs. To test focal male crabs at their home burrow an arena made of bamboo and sand-coloured fabric was placed around two neighbouring males and their burrows (Fig. 1). Neighbouring male pairs were selected

according to three criteria: (1) they were matched in claw size (estimated by visual comparison); (2) they were exhibiting courtship behaviour (courtship waving) indicating that they were actively defending a burrow; and (3) they were within one meter of one another (measured using a measuring tape stretched in a straight line from the center of one burrow to the other). Stimulus crabs captured from other areas of the mudflat were tethered with 10cm of clear monofilament line to bamboo posts inserted into the substrate within the arena to simulate wandering male crabs (intruders). This method of tethering stimulus crabs is relatively standard and has been used successfully in this and several other fiddler crab species to elicit both courtship and territorial behaviour as observed under natural conditions (Detto and Backwell, 2009; Detto et al., 2006; Detto et al., 2010; How et al., 2008; Milner et al., 2010; Pope, 2005; Reaney, 2007)(Booksmythe et al., 2010). Intruders were matched in claw size to focal crabs using visual comparison. Focal crabs were exposed to two 5-minute phases: a 'bystanding phase' (neighbour interacts with a simulated intruder) and a subsequent 'interaction phase' (focal male interacts with a simulated intruder) in one of four treatments (3 control and 1 experimental): (1) *null control* – no neighbour-intruder interaction in the 'bystanding phase' and no audience in the 'interaction phase' (n=11); (2) *audience control* – no neighbour-intruder interaction in the 'bystanding phase' and an audience in the 'interaction phase' (n=10); (3) *bystander control* – neighbour-intruder interaction in the 'bystanding phase' and no audience in the 'interaction phase' (n=11); and (4) *bystander and audience (experimental)* – neighbour-intruder interaction in the 'bystanding phase' and audience in the 'interaction phase' (n=11) (Fig. 1).

In the 'bystanding phase' of treatments (3) and (4) a stimulus male was tethered 40cm from the neighbour's burrow (min 90 cm from the focal male's burrow) and left for 5 minutes after both males (focal and neighbour) had emerged from their burrows. In the 'bystanding phase'

of treatments (1) and (2) the arena was approached (and stimulus male placement simulated) and the crabs were then left for 5 minutes after both males had emerged from their burrow. In the interaction phase a stimulus male was tethered 40cm from the focal male's burrow to simulate a wandering male. In treatments (2) and (4) the neighbouring male was allowed to emerge from his burrow and act as an audience while in treatments (1) and (3) the neighbouring male's burrow was blocked to prevent him from emerging during the trial period. Phases began when the focal or both males had surfaced (carapace and major claw visible), as applicable, and lasted for five minutes. Following a trial, burrows were marked with a small flag and within a semi-lunar tidal cycle these areas were avoided for further testing to ensure that males were not re-used over the course of the study. We quantified aggression as a behavioural state by measuring the duration of time that focal males were engaged in aggressive behaviours toward the simulated intruder in the 5-minute interaction phase. The observed aggressive behaviour, following previously published methods (see Burford et al., 2000; Oliveira et al., 1998; Wolfrath, 1993), included both non-contact aggression (threat displays) and that involving physical contact (pushing, grappling and tossing) and the intensity of enactment represents the focal male's willingness to escalate the contest (Oliveira et al., 1998; Wolfrath, 1993). We compared the time focal males spent performing aggressive behaviour among treatments with an analysis of variance with treatment as a fixed effect (SPSS v. 22). We included inter-burrow distance between the focal and neighbour as a covariate in the model as this varied across focal individuals. Post hoc analyses were carried out on the marginal means using a least significant difference adjustment for multiple comparisons. All behaviours were scored from video recordings (Panasonic HDC-SD800 camcorder) of the trials by a single observer (MKM) naïve to the trial condition.

160 The study was carried out under permit (ICNF, Portugal) following ethical approval from the
161 first author's home institution. All captured crabs were kept singly in shaded containers filled
162 with sea water and mud prior to testing and released back to their area of capture at the end of
163 a trial. Crabs were marked with non-toxic paint to ensure that they were not used more than
164 once in case of recapture.
165
166 **Results**
167
168 There was an overall effect of the treatment that focal males experienced on the amount of
169 aggressive behaviour they displayed toward a simulated intruder ($F_{3,38}$=11.797, p<0.0001,
170 Fig. 2). Our post hoc analysis revealed that there was an effect of having a neighbouring male
171 audience present during a territorial intrusion on the level of aggression expressed by a
172 burrow-holding male, but only if burrow-holding males had previously acted as bystander
173 (Treatment 4) to a neighbouring aggressive interaction (Table 1; Fig. 2). In short, males in
174 Treatment 4 behaved more aggressively than in any other treatment. Males in two of the
175 control treatments (Treatments 1 and 2) did not differ from one another in behaviour, but
176 males in the null control (no bystanding and no audience; Treatment 1), were less aggressive
177 than males in the bystander control (bystanding, no audience) (Treatment 3).
178
179 **Discussion**
180
181 Gleaning information from the social environment is essential for an individual to respond to
182 this environment appropriately (Danchin et al., 2004; Seppanen et al., 2007; Valone, 2007).
183 Individuals living in systems that are likely to be high in social noise will be under particular
184 pressure to either filter out information to avoid an inappropriate response or to use specific

cues to alert them to a situation where an active response may be required (e.g., Fitzsimmons et al., 2008; Naguib et al., 2004). This latter priming effect may be particularly important in predicting that, for example, a territorial challenge is likely to occur. The anticipation of being challenged is likely to affect not only how individuals respond to a rival conspecific during a direct interaction, but also how they respond to the presence of other conspecifics in the immediate environment. These individuals that are not part of the interaction, may themselves be gleaning social information (i.e. they are conspecific audiences). In this study we found the first evidence that a neighbouring male audience moderated male European fiddler crab behaviour towards an intruder, but only if males had acted as bystander to an aggressive interaction between a male neighbour and a same-sex intruder immediately prior to the encounter. This suggests that focal males that had viewed an aggressive interaction between his neighbour and an intruder were somehow primed for heightened responsiveness to having a male audience present during an interaction between himself and a territorial intruder. The observed increase in aggressiveness was likely also a function of a general priming for an aggressive response as a result of the bystanding, since we did detect greater aggressiveness when males without an audience had acted as bystander compared to males in our null control (no audience and no bystanding).

The prevalence of the use of public information (Danchin et al., 2004) suggests that it could be beneficial for individuals to employ strategies to manage the perceptions of unintended receivers. Fighting could communicate the focal male's motivation to defend his territory (Detto et al., 2010) or ability to do so (Peake et al., 2001) to his neighbour. However, we did not see an effect of a neighbouring male audience unless the focal male had previously acted as a bystander to an aggressive interaction between his neighbour and an intruder. Bio-regulatory mediators of the adjustment of aggressive behaviour are likely to be affected in

males that anticipate a territorial challenge based on cues in their social environment; facilitating an adjustment to an increased competitive environment with the appropriate behavioural response (Antunes and Oliveira, 2009). It could be that the simple presence of a neighbour is not enough of a cue of the extent of the competitive environment, given the ubiquity of territorial neighbours, and their familiarity, in a male's visual field (Detto et al., 2010; Hemmi and Zeil, 2003; Pope, 2005). Instead, if a territorial challenge has been observed immediately prior to an intrusion, effects on bio-regulatory mechanisms (Oliveira et al., 2001) could drive a response directly or at least provide a cue as to the probability of an escalation of aggression that could lead to a territorial takeover (Oliveira, 2009).

The bystander effect detected in this study is consistent with work in vertebrate species demonstrating increased levels of aggression (e.g., Clotfelter and Paolino, 2003), but inconsistent with the reverse priming demonstrated in another crustacean species (Zulandt et al., 2008). In our study, burrow holding males will have invested energy into establishing territory boundaries with their neighbours (Detto et al., 2010) and as such intruders are a potential threat to the territory more generally if they were to take over a neighbour's burrow. Zulandt and colleagues (Zulandt et al., 2008) suggest that the bystander effect could be resource dependent such that when resources are abundant, and consequently their value reduced, an individual will avoid escalation if the observation of a fight indicates that there is an increased likelihood of being challenged within their network. In the present study males were at their home burrow and as a consequence were defending a valuable resource; an added ecological realism that may have contributed to the direction of the effect.

Our study demonstrates that there is likely to be a complex interaction between audience and bystander effects in systems where individuals are part of a network of conspecific

interactants. The results suggest that selection has enhanced the use of public information to increase the appropriateness of responses to social stimuli. We investigated effects of the presence of a fiddler crab's nearest neighbour, an individual that the focal is likely to have interacted with before and to be familiar with, however, laboratory work on audience effects has demonstrated that attributes of an audience can influence physiological and behavioural effects on individuals, for example, sex and territorial status (Dzieweczynski et al., 2005). Future *in situ* work investigating behavioural reactions when the audience is a *non*-neighbour or a female, would therefore be particularly enlightening.

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357 Figure legends

358

359 Figure 1. Overview of experimental arenas and 4 treatments (3 control and 1 experimental)
360 used to investigate bystander and audience effects in male European fiddler crabs (see text for
361 details).

362

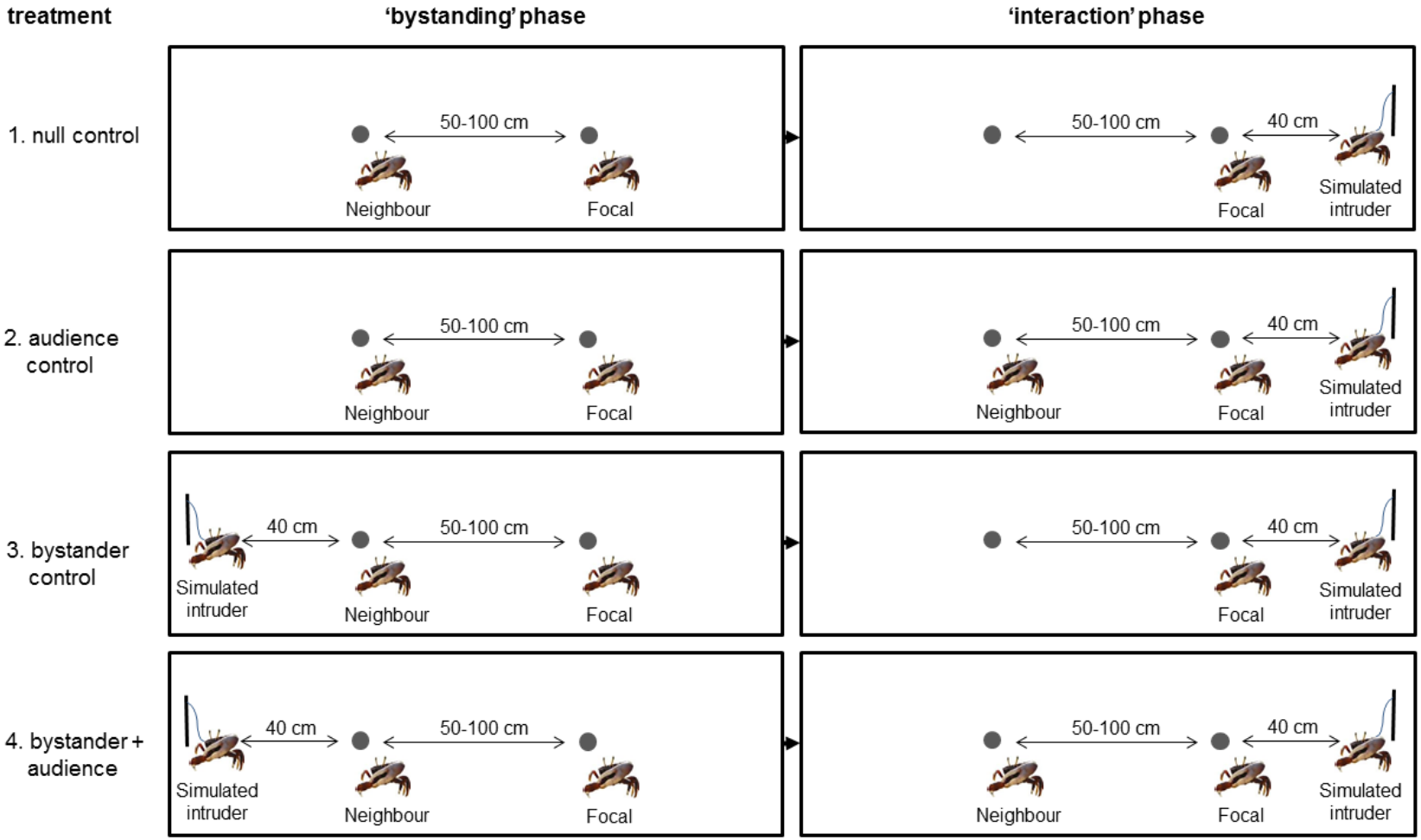
363 Figure 2. Average time that male European fiddler crabs spent engaging in aggressive
364 behaviour toward experimentally introduced male intruders in 4 social treatments (see Fig. 1)
365 designed to test for bystander and audience effects (Estimated Marginal Mean (EMM) ±SE;
366 matching letters indicate treatments where $p>0.05$ for tested differences).

367

Table 1. Results of the *post hoc* analysis of differences among treatments in burrow-holding male aggressive responses to simulated intrusions by conspecific male fiddler crabs. P-values in bold indicate where significant differences in aggressiveness were found.

			95% CI for Difference		
Treatment A	Treatment B	Mean difference	Lower bound	Upper bound	*P*
1 - Null control	2 - Audience control	-31.04	-82.41	20.33	0.229
	3 - Bystander	-53.73	-103.39	-4.07	0.035
	4 - Bystander and audience	-143.18	-194.50	-91.85	p<0.001
2 - Audience control	3 - Bystander	-22.69	-73.91	28.53	0.375
	4 - Bystander and audience	-112.14	-163.35	-60.92	p<0.001
3 - Bystander	4 - Bystander and audience	-89.45	-140.48	-38.42	0.001

373
374


treatment
'bystanding' phase
'interaction' phase
1. null control
2. audience control
3. bystander control
4. bystander + audience
50-100 cm
40 cm
Neighbour
Focal
Simulated intruder

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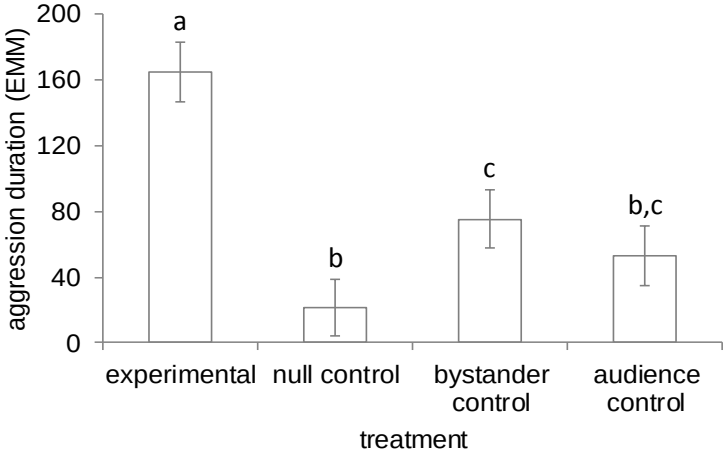
200
160
120
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aggression duration (EMM)
a
b
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b,c
experimental
null control
bystander control
audience control
treatment